

Life History and Cost Analysis for Continuous Rearing of *Perillus bioculatus* (Heteroptera: Pentatomidae) on a Zoophytogenous Artificial Diet

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ABSTRACT The impact of a zoophytogenous, insect-free artificial diet on the developmental rate, life history parameters, and fertility was examined over 11 consecutive generations for domesticated *Perillus bioculatus* (F.) (Heteroptera: Pentatomidae). This study showed that when fed an insect-free artificial diet during both the nymphal and adult stages, developmental times were prolonged, and the net reproductive rates (R_0) and the intrinsic rates of increase (r_m) were significantly lower than when fed larval *Trichoplusia ni* at both nymphal and adult stages. Moreover, the cost to rear *P. bioculatus* on the artificial diet approached 1.1 times the cost of rearing *P. bioculatus* on natural prey. These results demonstrate the effectiveness and potential cost-savings of the zoophytogenous artificial diet for rearing a beneficial pentatomid.

KEY WORDS beneficial insect, fecundity, cost efficiency, artificial diet

ALTHOUGH THE USE OF BENEFICIAL insects could displace insecticide use, the cost of beneficial insects is often too high to make their use a practical alternative. However, the development of artificial diets has the potential of reducing the cost of producing beneficial insects (Glenister 1998, Glenister and Hoffmann 1998, Ruberson and Coll 1998, Thompson 1999, Wittmeyer and Coudron 2001). This is especially true for those beneficial insects that are normally reared on host insects that are difficult to maintain in culture.

The twospotted stink bug, *Perillus bioculatus* (F.) (Heteroptera: Pentatomidae), is an example of a beneficial insect that can be difficult and costly to mass rear. This pentatomid is predaceous and native to North America (Knight 1952). It is able to feed on immature stages of species from several insect orders, but it has an intrinsic preference for the larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Saint-Cyr and Cloutier 1996). Most published reports of continuous rearing of *P. bioculatus* involve the use of secondary prey, such as lepidopteran larvae (Adams 2000, Yocum and Evenson 2002). One report (Rojas et al. 2000) discussed the results of testing two meridic diets as alternatives to insect prey. Another report (Yocum and Evenson 2002) discussed the com-

bination of a secondary prey and an artificial diet. However, none of the artificial diets reported were optimized for the continuous rearing of *P. bioculatus*, and both would most likely be limited to temporary use when the natural or secondary prey were not available or would require occasional supplementation with natural prey.

In a recent report, we described the continuous rearing of the beneficial pentatomid *Podisus maculiventris* (Say) on a new zoophytogenous artificial diet (Coudron et al. 2002). The developmental times, pre-oviposition periods, fecundity, and nymphal survival rates improved for a domestic colony and remained constant in a wild colony over 11 generations of rearing on the artificial diet. The realized cost associated with rearing either the domestic or wild colonies on the artificial diet approached the cost of rearing these insects on a natural prey. In this article, we report the life history and cost analysis of *P. bioculatus* on the same zoophytogenous artificial diet and discuss the impact of these results in the efforts to develop cost-effective methods to mass rear beneficial predators.

Materials and Methods

Insect Colonies and Diet. *P. bioculatus* eggs were obtained from the USDA-APHIS PPQ-MPPC (Mission, TX) and maintained at Biological Control of Insects Research Laboratory (Columbia, MO) for ≈ 20 generations. Experimental rearing conditions were $26 \pm 2^\circ\text{C}$, $65 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) h, maintained in a walk-in growth chamber.

The zoophytogenous artificial diet used in this study was a blended buffered mixture of ingredients from a

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meridic diet with beef and whole egg, encapsulated in a Mylar-Parafilm composite unit containing 40 μ l (Coudron et al. 2002). The natural prey used were live fourth instars of *Trichoplusia ni* (Hübner) that had been reared on a wheat-germ diet. Isolated individual prey-fed second and third instars, and fourth and fifth instars and adults were given one and two larvae per predator, respectively, every 24 h. Isolated individual diet-fed second and third instars, fourth instars, and fifth instars and adults were given one, two, and three diet instars, respectively, every 24 h (Coudron et al. 2000).

Experimental Design. Eggs and first and second instars were collected to begin the treatments (i.e., for both prey [*T. ni*] and diet [insect-free zoophytogenous artificial diet] treatments) as described previously (Coudron et al. 2002). The F1 generations of both prey-fed and diet-fed insects originated from the same generation of prey-fed parents. For the F1 generation of prey-fed and diet-fed insects, and the F6 and F11 generation of diet-fed insects, a random sample of 30 nymphs per treatment was weighed individually every 5 d, on day 0, 5, 10, and 15 postemergence of the second instar. Daily observations of development and mortality were made for all individuals. No replacement weights were taken for individuals that died during the experimental time. Molting, determined by the presence of exuviae, was recorded daily. By day 20 nymphs from each colony had emerged as adults. Nymphal developmental time was measured as time (days) within each stadium and time (days) from second stadium to adult eclosion. Life table values of l_x (number of individuals alive at beginning of stage x) and d_x (number of individuals dying in stage x) were obtained for each stage (x), and they were used to calculate stage-specific mortality and generational mortality of nymphs.

Individuals were sexed at adult emergence and weighed at 3 d postemergence for the F1 generation of prey-fed and F1, F6, and F11 generations of diet-fed insects. Five days after adult eclosion, 20 females were paired individually with a male of the same treatment for 8 h within each successive 48 h during a 12-d period. Mortality of females was recorded daily and dead individuals were not replaced. Dead males were replaced with virgin males of similar age and treatment. Eggs were collected daily for 12 d after the initiation of mating (up to 17 d postemergence of adult females). Eggs were counted, observed daily for hatch, and nymphs were observed until eclosion to the second instar. All life table and fertility table parameters were measured and calculated as described in Birch (1948) and Abou-Setta et al. (1986).

Statistical Analysis. All statistics were performed as described previously (Wittmeyer and Coudron 2001, Coudron et al. 2002). Rank transformed data for nymphal weight and developmental time were evaluated using a general linear model (GLM) to test the effects of treatment (i.e., treatment prey-fed and diet-fed as independent variables) with a significance level at $P = 0.05$. Stage-specific mortality and generation mortality were analyzed using a Log-Rank test, and a

GLM was used on rank-transformed data (i.e., female developmental time, preovipositional adult weight, preoviposition period, and eggs per female) to test the effect of treatments. Fertility table age-specific fecundity, m_x values (the number of female eggs laid per female at age x), include all fertile and infertile females to provide a more accurate estimate of net reproductive rate (R_0), mean generation time (T), and intrinsic rate of increase (r_m). The number of females evaluated for reproductive parameters per treatment was 20 per generation.

Analysis of Rearing Cost. The estimated cost of production was calculated using the same assumptions regarding colony size, test insects, and colony maintenance costs as described previously (Coudron et al. 2002). The total cost per generation (TCG) for all treatments was calculated by the following equation: $TCG = (n_e)(c_t) + (n_n)(c_f + c_t + c_d) + (n_a)(c_f + c_t + c_d)$, where n_e is number of days as eggs and first instar (7 d), c_t is cost per day to maintain *T. ni* colony (if prey-fed at any stage, then $c_t = \$3.21$; if diet-fed $c_t = \$0$), n_n is number of days as nymphs from molt of second instar to adult molt, n_a is number of days as adults (17 d for both prey-fed and diet-fed), c_f is cost to feed *P. bioculatus* when fed either food source (\$2.57), and c_d is cost per day to produce artificial diet (if prey-fed, then $c_d = \$0$; if diet-fed, then $c_d = \text{cost of diet production}$).

For all treatments, cost per egg (CPE) was then calculated by the following equation: $CPE = (TCG) / [(e)(f)(s)]$, where e is average number of eggs laid per fertile female; f is number of fertile females surviving to end of egg laying period, and s is proportion of eggs laid that survived molt to second stadium.

To evaluate the effect of intrinsic rate of increase upon the cost of colony maintenance, the doubling time (T_d , the number of generations required for the population to double in size) was calculated by the following equation: $T_d = [(\ln 2) / r_m] (1/T)$. The "realized" cost (the cost to double the population size) was determined as the total cost per generation multiplied by the T_d in units of generation.

Results

Effect of Artificial Diet on Nymphal Weight. The nymphal weights of prey- and diet-fed males were found to be significantly lower than females ($F = 9.91$; $df = 1, 344$; $P = 0.0018$). No significant difference was found between male and female nymphal weight analysis of variance (ANOVA) of diet-fed F1 ($F = 0.41$; $df = 1, 118$; $P = 0.5213$) and diet-fed F11 ($F = 1.50$; $df = 1, 112$; $P = 0.2231$). Prey-fed females demonstrated a faster increase in weight than males ($F = 10.02$; $df = 1, 112$; $P = 0.0020$). No significant difference was found between nymphal weights of diet-fed F1 and F11 insects ($F = 1.84$; $df = 1, 235$; $P = 0.1759$). Therefore, the data for diet-fed F1 and F11 were pooled for these analyses.

Significant treatment effects (Fig. 1) were found for nymphal weights between prey-fed and diet-fed insects ($F = 7.32$; $df = 1, 88$; $P = 0.0072$) at day 0 and for

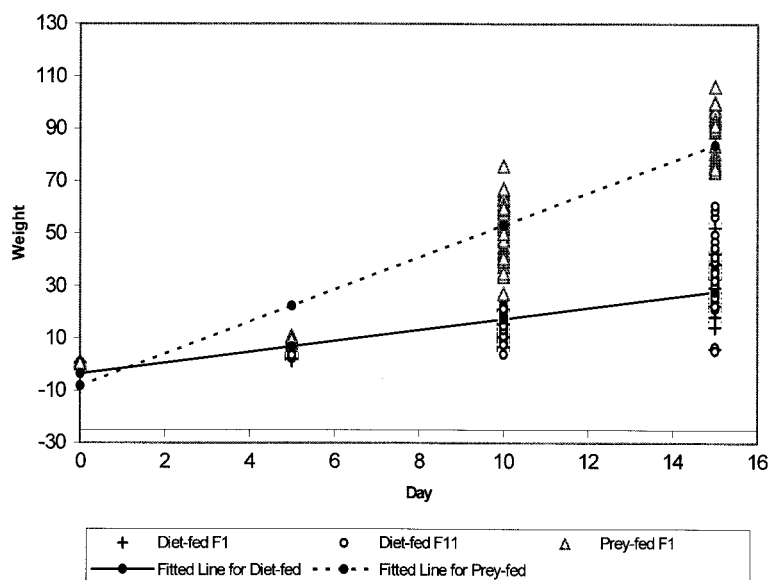


Fig. 1. Nymphal weights of F1 prey-fed and diet-fed and F11 diet-fed *P. bioculatus*. Data points represent means of each treatment.

the increase in weights over time ($F = 455.79$; $df = 1, 349$; $P < 0.0001$). The equations of fitted lines for a linear regression of \log_{10} -transformed nymphal weight data are diet-fed, $Y = -3.5526 + 2.0941(x)$ and for prey-fed, $Y = -8.1957 + 6.1304(x)$, where x denotes day and Y denotes weight. The slope values for the linear regressions indicated that the prey-fed insects gained weight faster than the diet-fed insects ($F = 455.79$; $df = 1, 349$; $P < 0.0001$).

Effect of Artificial Diet on Nymphal Survivorship. No mortality occurred in the prey-fed insects. Mortality occurred in the second, third, and fifth stadia of F1 and the third stadium of F11 diet-fed insects (Table 1). However, there was no significant difference in mortality among the prey-fed and diet-fed F1 and F11 insects (Log-Rank test: chi-square = 5.4739, $df = 2$, $P = 0.0648$).

Effect of Artificial Diet on Nymphal Developmental Time. No significant difference between male and female nymphal developmental time was observed during the 15-d observation period ($F = 0.006$; $df = 1$,

1010; $P = 0.7390$). Also, there was no significant difference between male and female nymphal developmental time when consideration was given to the interaction effect of food source and sex ($F = 0.11$; $df = 1, 238$; $P = 0.7390$; $F = 0.02$, $df = 1, 378$; $P = 0.8961$; and $F = 0.02$; $df = 1, 390$; $P = 0.8961$ for prey-fed, diet-fed F1, and diet-fed F11, respectively). Therefore, the data for male and female developmental times were combined for these analyses.

The nymphal developmental time was significantly shorter for F1 than for F11 diet-fed insects ($F = 32.6$; $df = 1, 778$; $P < 0.0001$). There was no significant difference in the developmental times during the second, third, and fourth instars ($F = 1.58$; $df = 1, 195$; $P = 0.2086$; $F = 0.006$; $df = 1, 193$; $P = 0.9461$; and $F = 0.47$; $df = 1, 193$; $P = 0.4960$, respectively) for F1 and F11 diet-fed insects. However, a significant difference occurred in the fifth instar ($F = 6.81$; $df = 1, 191$; $P = 0.0104$) between these two groups.

Significant treatment effects (Fig. 2) were found for nymphal developmental time between prey-fed and F1 and F11 diet-fed insects. The equations of fitted lines for a linear regression of \log_{10} -transformed nymphal developmental time data are prey-fed, $Y = 2.245 + 0.9117(x)$; for F1 diet-fed, $Y = 0.83 + 0.8533(x)$; and for F11 diet-fed, $Y = -1.811 + 2.5215(x)$, where x denotes days and Y denotes developmental time. The slope values for the linear regressions indicated the time spent during nymphal development was greater for F11 diet-fed insects than for prey-fed and F1 diet-fed insects ($F = 6.05$; $df = 1, 1016$; $P = 0.01$).

Effect of Artificial Diet on Adult Female Reproductive Parameters. There was no adult mortality of mated females, measured during the experimental pe-

Table 1. Stage-specific and generation mortality of *P. bioculatus* fed larval prey or a zoophytophagous diet

| Treatment | 2nd Instar ^a | 3rd Instar ^a | 4th Instar ^a | 5th Instar ^a | Generation mortality ^b |
|----------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-----------------------------------|
| Prey-fed F1 ($n = 60$) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diet-fed F1 ($n = 100$) | 3.0 | 1.0 | 0.0 | 1.0 | 5.0 |
| Diet-fed F11 ($n = 100$) | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 |

^a Stage-specific mortality = $(d_x / l_x) * 100\%$ d_x is the number of individuals dying in stage x , and l_x is the number of individuals alive at the beginning of stage x .

^b Generational mortality = $\sum_x (d_x / l_0) * 100\%$ d_x is the number of individuals dying in stage x , and l_0 is the number of individuals alive at the beginning of egg stage.

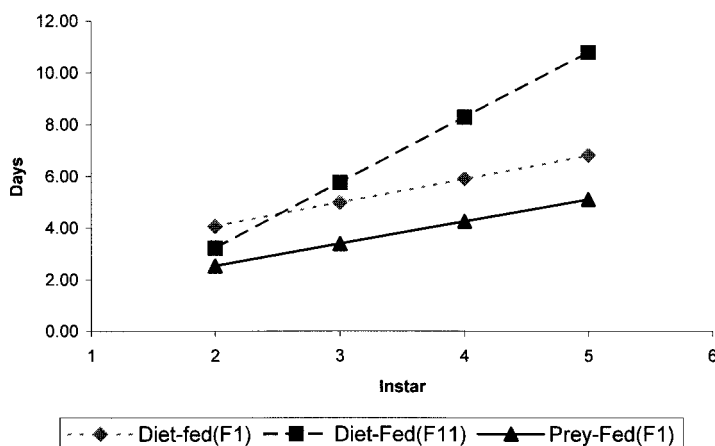


Fig. 2. Nymphal developmental time of F1 prey-fed and diet-fed and F11 diet-fed *P. bioculatus*. Data points represent means of each treatment.

riod for all treatments. There was a significant difference in cumulative developmental time to adult for females for all treatments ($F = 338.18$; $df = 3, 76$; $P < 0.0001$) used to measure reproductive parameters (Table 2). The adult weight was higher for prey-fed than for diet-fed females ($F = 42.15$; $df = 3, 76$; $P < 0.0001$), but there was no significant difference in female weights among diet-fed females (Table 2).

The mean preovipositional period differed significantly for prey-fed females compared with F6 diet-fed females, and for F1 diet-fed females compared with F6 and F11 diet-fed females ($F = 7.43$; $df = 3, 72$; $P = 0.0002$). There was no significant difference between the mean preovipositional period for prey-fed females compared with F1 and F11 diet-fed females, and F6 diet-fed females compared with F11 diet-fed females (Table 2).

The mean number of eggs laid per female during the first 17 d after adult emergence for prey-fed insects was 2.5–6 times higher than for diet-fed insects ($F = 36.19$; $df = 3, 74$; $P < 0.0001$). There was a significant and progressive increase in the mean number of eggs per female for F1 and F6/ F11 diet-fed insects (Table 2). However, there was no significant difference in the

mean number of eggs per female for F6 and F11 diet-fed insects.

Rearing on the artificial diet lowered the fertility of the F1 and F11 diet-fed females by $\approx 50\%$ compared with prey-fed females (Table 2). In contrast, the fertility of F6 diet-fed insects was lowered by only 15% compared with prey-fed females.

The R_0 value was 2.5 times higher for the prey-fed insects than for the diet-fed insects (Table 3). The R_0 increased for diet-fed insects over successive generations of being reared on the diet. The T value was lower for the prey-fed insects than for the diet-fed insects and increased in the F6 generation compared with the F1 and F11 generations for diet-fed insects. The r_m value was 3–5 times higher for the prey-fed insects than for the diet-fed insects. However, the r_m increased for diet-fed insects over successive generations of being reared on the diet.

Effect of Artificial Diet on Doubling Time and Cost of Rearing. Doubling time in generations (T_d) was shorter for prey-fed insects than for diet-fed insects and increased in the F6 generation compared with the F1 generation, but then it decreased in the F11 generation for diet-fed insects (Table 4). The total cost of

Table 2. Developmental time, adult weight, preoviposition, eggs per female and fertility of mated female *P. bioculatus*

| Treatment | Cumulative developmental time (d) ^a | Female weight (mg) ^b | Preoviposition ^c | Eggs/female ^d | Fertility ^e |
|-----------------------|--|---------------------------------|-----------------------------|--------------------------|------------------------|
| Prey-fed F1 (n = 20) | 15.35 \pm 0.49d | 96.65 \pm 6.34a | 6.40 \pm 0.50b,c | 151.1 \pm 28.39a | 1.00 |
| Diet-fed F1 (n = 20) | 19.70 \pm 0.57c | 81.23 \pm 4.83b | 5.40 \pm 0.58c | 23.75 \pm 34.08c | 0.45 |
| Diet-fed F6 (n = 20) | 24.40 \pm 1.36a | 80.72 \pm 4.89b | 10.5 \pm 0.23a | 45.44 \pm 37.39b | 0.85 |
| Diet-fed F11 (n = 20) | 20.75 \pm 0.96b | 78.46 \pm 6.67b | 8.44 \pm 1.15a,b | 63.55 \pm 36.46b | 0.50 |

Developmental time Female weight, Preoviposition, and eggs per female values are reported as Lsmean \pm SE developed from the GLM statistical analysis. Means for each treatment within same column followed by the same letter are not significantly different. This test was based on Fisher's least significant difference test.

^a Cumulative developmental time from second stadium to adult.

^b Female weight measured 3 d after adult emergence.

^c Number of days from emergence of adult to first oviposition.

^d Average eggs per female (fertile females only) collected from day 5 to day 17 postadult emergence.

^e Proportion of females that laid fertile eggs (eggs that hatch) per number of total mated pairs.

Table 3. Fertility table parameters for *P. bioculatus* maintained on larval prey or a zoophytophagous diet

| Treatment | Egg (R_0) ^a | Mean generation time (T) ^b (d) | Rate of increase (r_m) ^c (d^{-1}) |
|--------------|----------------------------|---|--|
| Prey-fed F1 | 59.68 | 18.27 | 0.2237 |
| Diet-fed F1 | 9.90 | 38.38 | 0.0590 |
| Diet-fed F6 | 15.55 | 45.58 | 0.0602 |
| Diet-fed F11 | 17.21 | 41.07 | 0.0692 |

^a $R_0 = \sum l_x m_x$ is the proportion of mated female alive at age x , and m_x is the average daily number of eggs laid by females of age x .

^b $T = (\sum x l_x m_x) / R_0$.

^c r_m is intrinsic rate of increase = $\sum \exp(-r_m * x) l_x * m_x$; where $r_m = \ln(R_0) / T$.

raw materials to rear one generation (TCG) was lower for prey-fed insects than for diet-fed insects, and again increased in the F6 generation compared with the F1 and F11 generations for diet-fed insects as a result of the T_d values. The cost per egg was lower for prey-fed insects than for diet-fed insects. However, the cost per egg decreased for diet-fed insects over successive generations of being reared on the diet. The higher number of eggs laid, shorter mean generation time, and faster doubling time for prey-fed insects resulted in lower values for the cost per egg and the cost to double population size (the realized cost of rearing) than for diet-fed insects. The realized cost of rearing was lowest for the prey-fed insects, but it was closely approximated by the diet-fed insects in the F6 generation (Table 4; Fig. 3).

Discussion

Mortality was low throughout this study and was limited to the nymphal stage of diet-fed insects, being most pronounced in the first generation on the diet. Weight gain in diet-fed nymphs during both the F1 and F11 generations was slower than that in prey-fed nymphs. It is interesting to note that the pattern of weight gain in F11 diet-fed insects was comparable with that in F1 diet-fed insects, suggesting that no, or minimal, adaptation or selection had occurred. Additionally, the developmental time to adult was extended for insects reared on the zoophytophagous diet and became more prolonged with successive generations reared on the diet. Both the net reproductive rate

Table 4. Doubling time and cost of rearing for *P. bioculatus* reared on larval prey or a zoophytophagous diet

| Treatment | Doubling time (T_d) ^a (generations) | TCG ^b (\$) | Cost/egg ^c (\$) | Cost of doubling ^d (\$) |
|--------------|--|-----------------------|----------------------------|------------------------------------|
| Prey-fed F1 | 2.87 | 208.27 | 0.0133 | 32.79 |
| Diet-fed F1 | 11.24 | 225.70 | 0.2133 | 65.29 |
| Diet-fed F6 | 15.76 | 254.61 | 0.0746 | 35.69 |
| Diet-fed F11 | 9.90 | 232.16 | 0.0739 | 55.98 |

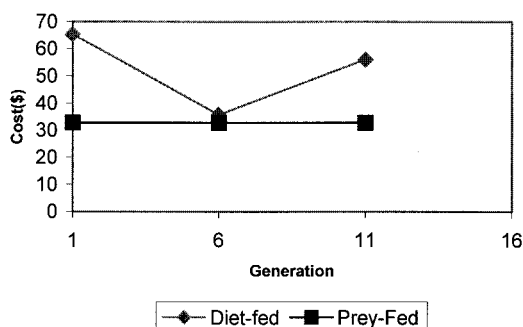
^a T_d doubling time = $[(\ln 2) / r] / (1/T)$.

^b TCG, cost of raw material required to rear one generation.

^c Cost/egg: $TCG / (e^{f * n} * a * s)$.

^d Cost of doubling: $TCG * (T_d \text{ generation})$, where T_d generation is $\ln(2) / (r_m * T)$, and T is mean generation time (see Table 3).

The cost of Doubling

**Fig. 3.** Cost of doubling of prey-fed and diet-fed *P. bioculatus*.

and intrinsic rate of increase were negatively impacted by the artificial diet. However, both of these values improved with subsequent generations of rearing on the diet. Consequently, the cost per egg was highest for the early generations on the diet.

To evaluate the true efficacy of the zoophytophagous diet for the continuous rearing of *P. bioculatus*, the estimated cost of raw materials and labor to produce the diet was incorporated into a realized cost of rearing (Thompson 1999, Coudron et al. 2002). The lower cost of materials for the artificial diet compared with the cost of raising the lepidopteran host (*T. ni*) offset the added cost of prolonged development and reduced fecundity in the diet-fed insects, such that by the F6 generation the realized cost of rearing on this artificial diet approximated rearing on natural prey. However, a decrease in fertility in the diet-fed insects in the F11 generation caused the realized cost to rise above that for the prey-fed insects.

A direct comparison of the performance of *P. bioculatus* on the zoophytophagous diet with other artificial diets that have been tested previously (Adams 2000, Rojas et al. 2000, Yocum and Evenson 2002) is not possible. However, the low cost of the zoophytophagous diet and the comparison of rearing to a low-cost prey, e.g., *T. ni*, are a benefit of this study compared with the cost of other diets and host insects tested. The sustained performance over successive generations on this diet is encouraging and the expectation is that the zoophytophagous diet will perform well as a substitute for the insect prey currently used for continuous rearing of *P. bioculatus*.

A comparison can be made between the performance of *P. maculiventris* (Coudron et al. 2002) and *P. bioculatus* when reared on the zoophytophagous diet. Survivorship and the ability to rear for successive generations on the artificial diet was high for both species. The number of eggs per female and intrinsic rate of increase was higher for *P. maculiventris* than for *P. bioculatus* when reared on the diet. The cost of doubling was higher for both species when diet-reared compared with the prey-fed. However, the performance of *P. maculiventris* approached that of prey-fed

after 11 successive generations when reared on the diet. A wild colony (i.e., field specimens) of *P. maculiventris* performed better at the measured parameters on the artificial diet than did a laboratory colony (i.e., domesticated specimens), suggesting that better results may be obtained by mass rearing a wild colony. Unfortunately, a wild colony of *P. bioculatus* was not available for this study, but it would be interesting to determine whether a wild colony of *P. bioculatus* would show the same increase in the cost of doubling after 11 successive generations of being reared on the diet as was observed in the laboratory colony used in these studies.

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